

EXOTIC PLANTS AT THE DESERT LABORATORY, TUCSON, ARIZONA

TONY L. BURGESS, JANICE E. BOWERS, and RAYMOND M. TURNER
U.S. Geological Survey, Research Project Office,
1675 West Anklam Road, Tucson, AZ 85705

ABSTRACT

A census and mapping of the exotic flora of the Desert Laboratory grounds, Tucson, Arizona, is described. Most of the 52 exotic species are restricted to disturbed habitats. Five annuals (*Bromus rubens*, *Erodium cicutarium*, *Hordeum murinum*, *Sisymbrium irio*, and *Schismus* sp.) and one perennial grass (*Pennisetum ciliare*) have invaded extensive areas of undisturbed Sonoran Desert vegetation. Shared features of these six species are discussed with respect to climates of origin, evolution with pastoralism, grazing history of southern Arizona, integration into native food webs, and reproductive biology. The invasions appear to be irreversible, and other exotic species show signs of becoming increasingly invasive. What has occurred on the Desert Laboratory grounds may represent the future pattern for much of the eastern Sonoran Desert. The present status and history of introduction of each exotic species are presented in an appendix.

In 1903 the Carnegie Institute of Washington established the Desert Laboratory at Tucson, Arizona, to investigate desert plant ecology (Coville et al. 1903). Soon afterwards, Spalding (1909) mapped the distribution of two exotic plant species, *Erodium cicutarium* and *Hordeum murinum*, on the Desert Laboratory grounds. *Cynodon dactylon* was the only other exotic in the Desert Laboratory flora (Spalding 1909). Since then, exotic species have proliferated, and the total is now 52 (Bowers and Turner 1985; Turner and Bowers 1988).

Much research on exotic plants in the North American deserts has concentrated on disturbed habitats. In the Great Basin, Eurasian annuals such as *Salsola australis*, *Bromus tectorum* L., *Sisymbrium altissimum* L., and *Descurainia sophia* (L.) Webb. naturalized in sagebrush scrub following intensive burning and grazing (Piemeisel 1951; Young et al. 1972; Yensen 1981; Mack 1981, 1986). In the Sonoran Desert, *Salsola australis*, *Schismus* spp., *Sisymbrium irio*, *Bromus rubens* and *Erodium cicutarium* colonized abandoned farmland (Karpiscak 1980). *Erodium cicutarium* and *Bromus rubens* established on land that had been denuded of vegetation but not plowed in the Mojave Desert (Piemeisel 1932) as well as on other disturbed sites (Rickard and Sauer 1982). Less attention has been paid to establishment of exotics in undisturbed desert communities. Beatley's (1966) study of *Bromus* species in the Mojave Desert is a notable exception. The goal of the present study was to document the status

and history of exotic plants at the Desert Laboratory, particularly those naturalized in undisturbed habitats.

STUDY AREA

The Desert Laboratory grounds include Tumamoc Hill and the level to gently rolling plain to the west, 352 ha in all (Fig. 1). A rocky outlier of the Tucson Mountains, the hill rises 245 m above the surrounding plain to an elevation of 948 m and is composed of Tertiary volcanics. Adjacent lower areas contain alluvial deposits of varying ages and outcrops of Cretaceous clay.

The climate features mild winters, hot summers and biseasonal precipitation. Afternoon temperatures from June through September often exceed 38°C. Minimum temperatures on the hill may remain above freezing in a mild winter or drop as low as -8.9°C in the coldest ones. In the rather severe winter of 1931-1932, there were 18 freezing nights on the hill (Turnage and Hinckley 1938). Yearly rainfall from 1904 to 1980 averaged about 250 mm/year. About half of the yearly total comes during July, August and September. Most of the remainder falls between October and April.

Study-area vegetation is typical of the Arizona Upland Subdivision of the Sonoran Desert (Shreve 1951). Dominants include *Cercidium microphyllum* (Torr.) Rose & I. M. Johnst., *Larrea tridentata* (DC.) Cov., *Opuntia versicolor* Engelm., *O. phaeacantha* Engelm., *Fouquieria splendens* Engelm., *Lycium berlandieri* Dun., *Encelia farinosa* Gray, and *Ambrosia deltoidea* (Torr.) Payne. Along the washes *Cercidium floridum* Benth., *Prosopis velutina* Woot., *Acacia constricta* Benth., and *A. greggii* Gray are common. Spalding (1909) and Goldberg and Turner (1986) provide more detailed descriptions.

Grazing on the Desert Laboratory grounds ceased when the property was fenced in 1907. Before then, cattle and goats fed "in considerable numbers" on Tumamoc Hill (Bowers 1989). Grazing was severe enough that after four years of protection, Thornber detected "a marked increase in the perennial grasses," notably *Hilaria mutica* (Buckl.) Benth., *Hilaria belangeri* (Steud.) Nash, *Bouteloua curtipendula* (Michx.) Torr., and *Muhlenbergia porteri* Scribn. (Thornber 1910, p. 292). After fencing, the grounds were little disturbed until the 1950's, when easements were granted for three gas pipelines and three electric powerlines. Other localized disturbances in the past three decades have included a sanitary landfill and a clay quarry (both now abandoned) and several roads.

Despite these local alterations, the Desert Laboratory grounds, situated 5 km west of downtown Tucson, have been stable relative to their environs. In 1910 Tucson's population was 13,913 and its urban area was 3.1 km² (Bufkin 1981). North and east of the Desert Laboratory were cultivated fields; south and west lay undeveloped

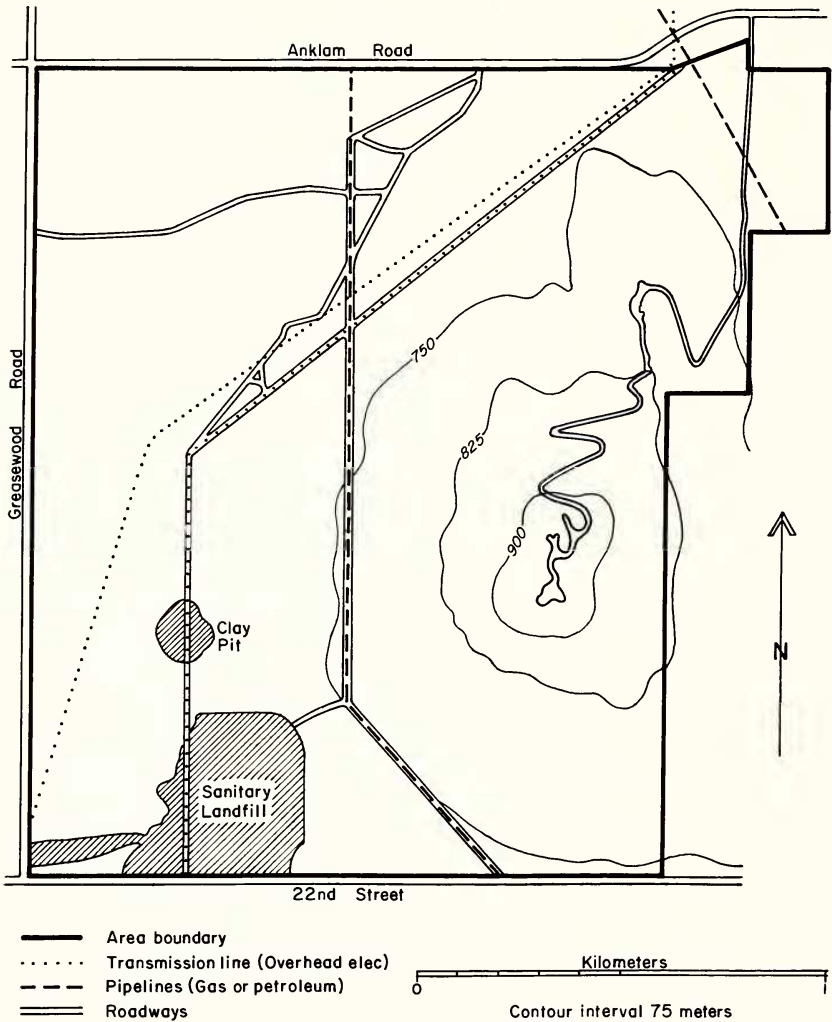


FIG. 1. Map of Desert Laboratory showing boundaries, paved road, outline of landfill and washes.

desert. By 1980 Tucson's urbanized area held approximately 500,000 people in 324 km², and the Desert Laboratory grounds were almost surrounded by suburban developments.

SURVEY FOR EXOTIC PLANTS

We surveyed the Desert Laboratory grounds for exotic plants from February to June of 1983. We marked gridlines on aerial photo-

graphs (scale 1:2256) of the property, then, using the photographs as a guide, we walked each gridline, remaining on it insofar as possible. The gridlines were 226 m apart and had a total length of about 40 km. We recorded the Cartesian coordinates and relative abundance of all exotic plants encountered within about 2 m of the lines. We also surveyed the paved road (Fig. 1) and all other disturbed or artificial habitats not intersected by the grid. Using the coordinates, we generated a distribution map for each species encountered. In the course of this survey we found 33 of the 52 exotics in the flora (Appendix 1). The remainder are so infrequent that our survey grid did not intersect them.

RESULTS AND DISCUSSION

Localized exotics. A few of the exotics recorded during our survey are restricted to particular, usually artificial, habitats. These include such species as *Phalaris minor* and *Polygogon monspeliensis*, known from ephemeral ponds at the landfill, and *Salsola australis*, abundant on dry, disturbed landfill substrates. *Salsola* seeds cannot germinate once the soil has formed a crust; thus the species is most characteristic of recently disturbed sites (Karpiscek 1980).

Many more exotics, while local in distribution, can be identified with no particular habitat. Some apparently require soil disturbance. *Matthiola longipetala* is occasional on the landfill and nearby roadsides, whence it is spreading to disturbed habitats nearby. Others seem not to need disturbed seedbeds and may eventually spread extensively. In the 30 years since *Brassica tournefortii* first appeared near Yuma, Arizona (Mason 1960), it has established along roads and in undisturbed desert in western Arizona. On the Desert Laboratory grounds, this species is especially abundant along the western boundary fence line whence it is colonizing the grounds using washes as corridors. *Dimorphotheca sinuata*, an ornamental annual commonly cultivated in Tucson, is invading from the southwest edge of the property, where it has doubtless escaped from cultivation in a nearby housing development. Like *Brassica*, *Dimorphotheca* spreads along washes.

The process of introduction continues. Two exotics appeared on the grounds after the 1983 survey—*Caesalpinia gilliesii* and *Opuntia microdasys*. Both are common ornamentals in nearby yards and gardens.

Naturalized exotics. Five exotic annuals and one exotic perennial have naturalized on our study area; that is, they self-seed in undisturbed habitats and occur as frequently as common native species. *Erodium cicutarium* and *Hordeum murinum* occupied scattered patches on the northwest side of the Tumamoc Hill property in 1906 (Sapling 1909). Both have since naturalized throughout the grounds

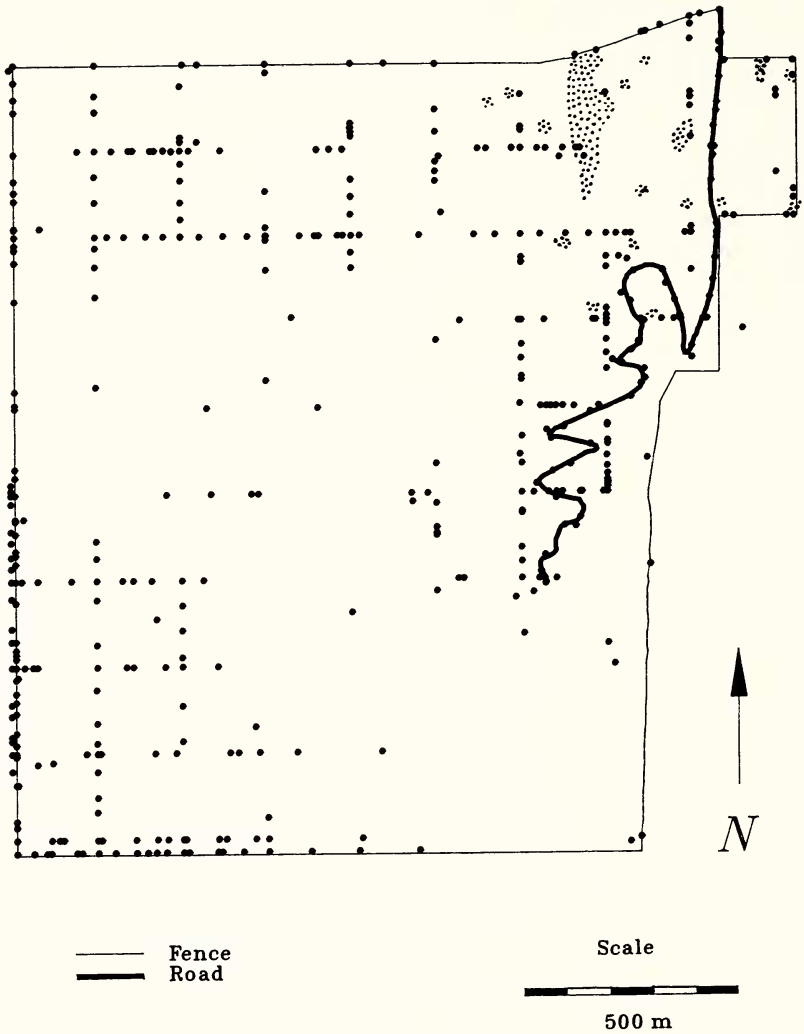


FIG. 2. Distribution of *Erodium cicutarium* at Desert Laboratory in 1906 (stippled areas) and 1983 (dots). From Turner and Bowers (1988).

(Figs. 2, 3). *Sisymbrium irio*, *Bromus rubens*, and *Schismus* spp. have also naturalized on our study area, apparently within the last 50 to 76 years (Appendix 1). *Pennisetum ciliare*, a perennial grass, forms colonies up to 20 m across on rocky slopes of Tumamoc Hill and is also common along some washes. It has spread steadily since our 1983 survey and, like the six exotic annuals, establishes well in undisturbed habitats.

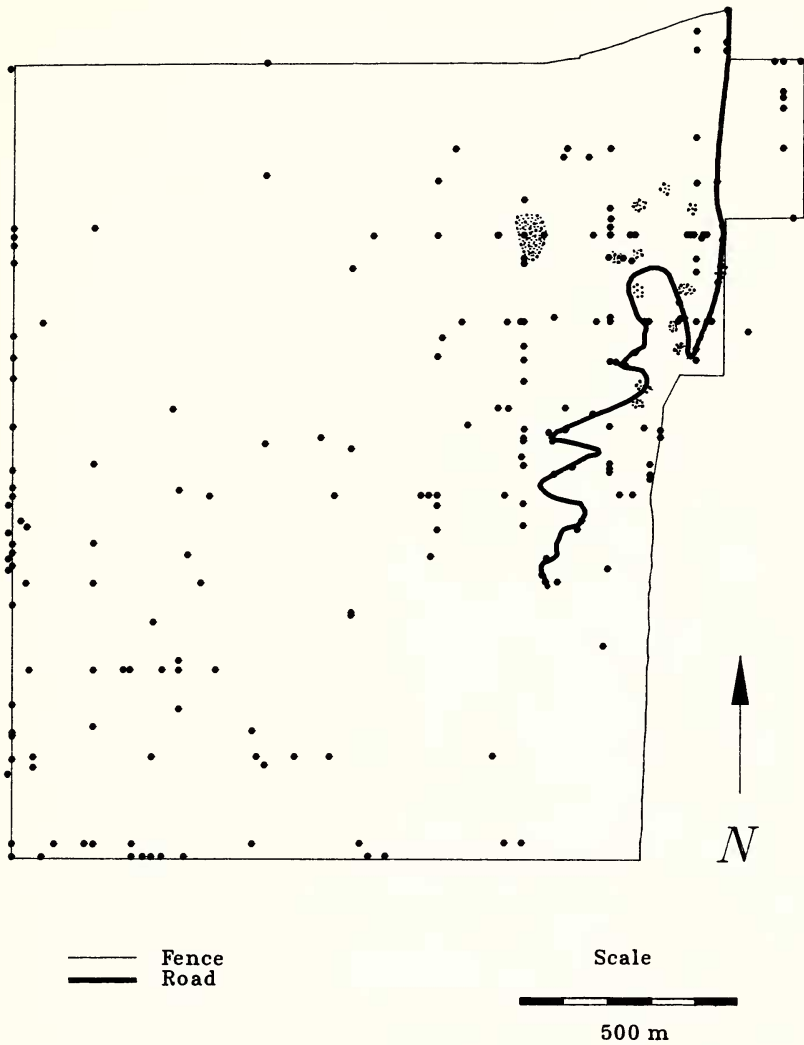


FIG. 3. Distribution of *Hordeum murinum* at Desert Laboratory in 1906 (stippled areas) and 1983 (dots). From Turner and Bowers (1988).

Why have these seven exotics been able to invade habitats that have undergone no appreciable disturbance for decades? We offer several mutually dependent explanations: favorable climate, prior evolution in regions with intensive pastoralism, the grazing history of southern Arizona, minimal integration into native food webs, and reproductive biology.

Climate. Exotics typically naturalize where climate and vegetation

are similar to those of their source areas (Baker 1986). Biseasonal rainfall and subtropical temperatures make the northeastern Sonoran Desert vulnerable to two separate legacies of human landscape alteration: the "Mediterraneanization" of California (Heady 1977; Le Houerou in press) and the "Africanization" of the Neotropics (Baker 1978; Parsons 1970).

The six naturalized annuals on our grounds are native to the Mediterranean region and the Near East, where they grow in winter-rainy climates. *Bromus rubens* ranges from Asia Minor through the Mediterranean region (Tsvelev 1983), where it occurs in natural steppe vegetation and cultivated fields (Feinbrun-Dothan 1986; Hubl and Holzner 1982; Ayyad and Ammar 1974). Since its introduction in the mid-1880's, the species has spread from California to Texas and south into Baja California (Correll and Johnston 1970; Gould and Moran 1981). Its virtual absence from the Great Basin is probably related to sensitivity to frost (Hulbert 1955). *Schismus barbatus* and *S. arabicus*, both highly successful invaders in the Mojave and Sonoran deserts, grow in a variety of arid and semi-arid vegetation types as well as in disturbed sites from the Mediterranean through the Near East (Conert and Turpe 1974; Feinbrun-Dothan 1986). *Hordeum murinum* typically grows in disturbed, ruderal sites (Davison 1971; Frenkel 1977; Zohary 1973) or cultivated fields (Tadros and Atta 1959; Zohary 1950). It does not often dominate in stands of perennial vegetation in its native Eurasia, but it can be a common component of annual pastures elsewhere, as in Australia (Rossiter 1966) and California (Heady 1977; Jackson 1985). *Erodium cicutarium* can be found in disturbed or open habitats over most of Eurasia (Webb and Chater 1968; Vvedenskii 1974; Zohary 1972). It was among the earlier invaders in California (Heady 1977; Wester 1981). Various forms in the *Sisymbrium irio* complex can be found from Europe to India (Khoshoo 1955, Titz 1969). The species spread from southern to northern Europe during the seventeenth through nineteenth centuries (Ball 1964; Ellenberg 1988; Salisbury 1964), more or less concurrently with its colonization of North America.

The Africanization of our study site is evident in the establishment of the introduced perennial grass *Pennisetum ciliare*, which is native from northwestern India through the Middle East to southern Africa (DeLisle 1963). Coming from an area where climates are subhumid to arid with predominantly warm-season rainfall, *P. ciliare* is well adapted to exploit soil-moisture regimes typical of the summer and fall in southern Arizona (Cox et al. 1988). Although present on our study area since at least 1968, this species did not become extensively naturalized until the 1980's, after two periods of unusually wet summers. During the first of these, from 1970 to 1972, warm-season (October-May) rainfall exceeded the average (186 mm) by 103, 128 and 119 mm, respectively. During the second, from 1982 to 1984,

warm-season totals were 134, 200 and 116 mm, respectively, above the average. Undoubtedly the more recent wet interlude and perhaps also the earlier one contributed to the increase of *P. ciliare*. Climatic fluctuations may also promote invasions by causing mortality of established natives, thereby creating openings for establishment (Tisdale et al. 1965). On slopes where *P. ciliare* has been invading, there has been considerable mortality of *Encelia farinosa*, apparently caused by freezing.

Evolution with pastoralism. The pattern of invasions between arid habitats in the Old and New worlds is not symmetrical. New World annuals and grasses have not become widely established outside of ruderal sites in either North Africa (Le Floch et al. 1990, Le Houerou in press) or southern Africa (Brown and Gubb 1986). Highly disturbed ruderal and segetal conditions developed earlier and more extensively in the Old World (Diamond 1988). While the emerging symbiosis among humans, large domestic animals and crops subjected Old World floras to selection under increasing disturbance (Jackson 1985; Naveh 1967; Young et al. 1972), Holocene vegetation in North America developed with a significantly reduced megafauna (Martin and Klein 1984) and no pastoralist societies. These contrasting histories resulted in the Sonoran Desert having relatively few species adapted to intensive grazing in comparison with floras from similar climates in the Old World.

Grazing history. There are strong connections between invasions of exotic plants and the advent of widespread pastoralism in the Sonoran Desert. The pattern of overgrazing on Arizona rangelands around the turn of the century has been well-documented (Wagoner 1952; Bahere and Bradbury 1978). The drought of 1890–1892, one of the worst on record for Arizona, aggravated the effects of overgrazing (Bahre and Bradbury 1978). By 1910, the desert grassland had been denuded of perennial grasses, and native annuals such as *Aristida adscensionis* and *Bouteloua aristidoides* had replaced them (Griffiths 1910).

Exotic annuals also increased as perennial grasses declined. *Erodium cicutarium* appeared in the San Pedro Valley east of Tucson by 1880 (Arizona Daily Star, February 10, 1880) and in the Sulphur Springs Valley by 1866 (Thornber 1906). By 1903 this species was locally naturalized on overgrazed ranges south of Tucson (Thornber 1903), and by 1910, *Hordeum murinum* was also becoming established on ranges in the vicinity (Thornber 1910). Range managers deliberately introduced certain exotic species. *Bromus rubens* was one of 24 annual forage species sown on the Santa Rita Experimental Range south of Tucson in the winters of 1906–1907 and 1907–1908 (Thornber 1910). *Erodium cicutarium* was also sown by at least one rancher (Arizona Daily Star, June 13, 1880).

The timing of these events strongly suggests that overgrazing fostered establishment of exotic annuals on southern Arizona ranges. A similar process has been implicated in California, where decades of overgrazing removed the native cover, leaving the land vulnerable to colonization of exotics (Biswell 1956; Naveh 1967; Frenkel 1977; Wester 1981). Although we have no quantitative evidence regarding the history of livestock on the Desert Laboratory grounds, it is likely that grazing before 1907 favored the establishment of exotics in the vicinity.

This is not to say that disturbance by pastoralism is the sole cause of invasions. McKell et al. (1962) suggested that communities of annual plants—such as those in the deserts of California—are “extraordinarily open.” In 1986, after a drier than normal winter, we first detected *Schismus* sp. and *Brassica tournefortii* on the floor of MacDougal Crater in northwestern Sonora, Mexico. The crater is inaccessible to domestic livestock, and anthropogenic disturbance has been limited to occasional visits by botanists and others. This and similar examples suggest that Sonoran Desert communities are relatively open to invasion by Old World exotics. Such “openness” may result from a combination of factors, among them an initial lack of integration into food webs, the reproductive biology of invading species and competitive effects.

Integration into food webs. An invading species, particularly one from another continent, is unlikely to meet resident pathogens or predators adapted to exploit it intensively. Exotic plant species may profit from a period free of such biotic checks as diseases and insects, as noted by McKell et al. (1962) for the grass *Taeniatherum asperum* (Simonaki) Nevskii. Even highly palatable invaders may be ‘hidden’ when outnumbered by other species (Risch and Carroll 1986). Once an invading plant increases, evolutionary and behavioral responses of consumers and pathogens begin to integrate it into the food web, and its initial advantage declines. Seeds of *Erodium cicutarium*, for example, are heavily used by native granivores (Inouye et al. 1980; Soholt 1973; Stamp and Ohmart 1978; De Vita 1979). Herbivore effects are not always negative, however; in many cases, native consumers are effective dispersal agents (Knight 1986; Rissing 1986).

Reproductive biology. With the possible exception of *Sisymbrium irio*, the naturalized exotics on our study site are apparently self-compatible or apomictic (Booth and Richards 1976; DeGroot and Sherwood 1984; Faruqi and Quraish 1979; Martin and Harding 1982; Wu and Jain 1978), conforming with Baker’s (1955) observations on successful weeds.

Most native annuals studied to date show relatively precise requirements for germination (Went 1948, 1949; Went and Westergaard 1949; Juhren et al. 1956; Tevis 1958), so that in a given year

there are seldom enough temperature-moisture combinations to germinate all the species in the seed bank (Juhren et al. 1956). Many require a rainfall event of more than 25 mm to germinate (Beatley 1974). Germination requirements of the naturalized exotics appear to be less precise. Thus, in years unfavorable for germination of native annuals, such exotic species as *Bromus rubens*, *Sisymbrium irio* and *Schismus barbatus* still establish and reproduce in favorable microsites.

Some native annuals may have density-dependent germination (Inouye 1980) whereby the presence of established plants on a site prevents others from germinating. *Bromus rubens*, *Hordeum murinum* and *Schismus barbatus* do not suppress germination at high densities (Wu and Jain 1979; Szarek et al. 1982; Borchert and Jain 1978; Davison 1971). After good rains, mass germination in these species produces dense stands that suppress other ephemerals.

Seeds of *Erodium* and *Sisymbrium* can have extended dormancy (Roberts 1986; Wilson and Duff 1984). In contrast, *Schismus*, *Hordeum* and *Bromus* do not normally form long-lasting seed banks (Loria and Noy-Meir 1980; Popay 1981; Roberts 1981; Wu and Jain 1979). Populations build up rapidly during a series of good years, but a bad season can cause catastrophic losses. Following a poor year, seeds are dispersed into depleted areas from individuals that reproduced in more mesic sites.

In short, the lack of specificity in germination requirements, the ability to reproduce under intense crowding and marginal conditions, and effective seed dispersal are critical factors in the successful naturalization of certain exotics at the Desert Laboratory.

Competitive effects. Whether naturalized annuals are crowding native species out of the habitat is unknown. The native *Erodium texanum* is a common associate of *E. cicutarium* at the Desert Laboratory. Inouye et al. (1980) indicate possible competition between the two.

It appears that *Pennisetum ciliare* is displacing *Encelia farinosa* from some rocky slopes. The root systems of both exploit the upper soil horizons (Cannon 1911; Christie 1975), but some temporal partitioning of soil moisture should exist. *Pennisetum* is most active during the warm season whereas *Encelia* grows in late winter and spring. *Encelia* has not reestablished within larger stands of *Pennisetum*. Apparently a temporary competitive release can start a *P. ciliare* invasion (Danin 1976) which may be consolidated by allelopathic effects (Cheam 1984; Hussain et al. 1982).

Because *Pennisetum ciliare* tolerates burning better than most long-lived Sonoran Desert perennials (Mayeux and Hamilton 1983; Mott 1982; Mannelje et al. 1983), occasional fires may promote its increase at the expense of native species. *Bromus rubens* can

produce substantial biomass, particularly during wet winters (Beatley 1969; Bowers 1987). The resulting dry litter seems to promote the spread of fires that restructure the perennial vegetation without adversely affecting *B. rubens* (Beatley 1966; Brown and Minnich 1986; Rogers and Steele 1980).

CONCLUSIONS

Though much of the Desert Laboratory grounds has been protected for decades, certain exotic plant species occur throughout the property on disturbed and undisturbed sites alike. Winter annuals from the Mediterranean and Near East predominate in the exotic flora, whereas introduced summer annuals play a minor role. The changes that have occurred over the last 50 to 75 years appear irreversible. Grazing before 1907 could have created conditions that favored the initial invasion by exotic annuals. Exotic perennial grasses were introduced later (Cox et al. 1988), and their invasion appears to be accelerating. The most successful exotics, whether annual or perennial, share features that indicate evolution in ruderal habitats in climates similar to that of the Sonoran Desert.

The character and rate of change in the Desert Laboratory flora have undoubtedly been influenced by its proximity to the rapidly growing city of Tucson, which has often served as a source of propagules. Parts of the Sonoran Desert remote from urban centers have not undergone the rapid proliferation of exotics seen at the Desert Laboratory; nevertheless, the invasion of relatively undisturbed habitats within the grounds indicates a possible future of Sonoran Desert vegetation.

ACKNOWLEDGMENTS

We thank Robert Webb and John Steiger for assistance with field work, Conrad Bahre for suggestions regarding history of introduction, Paul Martin for suggestions on asymmetrical histories, and our thoughtful reviewers: Richard Mack, Jerry Cox, and Peter Warshall.

LITERATURE CITED

- Arizona Daily Star, February 10, 1880.
———. June 13, 1880.
- AYYAD, M. A. and M. Y. AMMAR. 1974. Vegetation and environment of the western Mediterranean coastal land of Egypt, 2. The habitat of inland ridges. *Journal of Ecology* 62:439-456.
- BAHRE, C. J. and D. E. BRADBURY. 1978. Vegetation change along the Arizona-Sonora boundary. *Annals of the Association of American Geographers* 68:145-165.
- BAKER, H. G. 1955. Self-compatibility and establishment after "long-distance" dispersal. *Evolution* 9:347-348.
- . 1978. Invasion and replacement in Californian and Neotropical grasslands. Pp. 368-384 in J. R. Wilson (ed.), *Plant relations in pastures*. CSIRO, East Melbourne, Australia.

- . 1986. Patterns of plant invasion in North America. Pp. 44–57 in H. A. Mooney and J. A. Drake (eds.), *Ecology of biological invasions of North America and Hawaii*. Springer-Verlag, New York.
- BALL, P. W. 1964. *Sisymbrium* L. Pp. 264–266 in T. G. Tutin, V. H. Heywood, N. A. Burges, D. H. Valentine, S. M. Walters, and D. A. Webb (eds.), *Flora Europaea*, Vol. 1. Cambridge University Press, Cambridge.
- BAUM, B. R. and L. G. BAILEY. 1984a. Taxonomic studies in wall barley (*Hordeum murinum*) and sea barley (*Hordeum marinum*). 1. Character investigation: assessment of new and traditional characters. *Canadian Journal of Botany* 62:753–762.
- and ———. 1984b. Taxonomic studies in wall barley (*Hordeum murinum* sensu lato) and sea barley (*Hordeum marinum* sensu lato). 2. Multivariate morphometrics. *Canadian Journal of Botany* 62:2754–2764.
- BEATLEY, J. C. 1966. Ecological status of introduced brome grasses (*Bromus* spp.) in desert vegetation of southern Nevada. *Ecology* 47:548–554.
- . 1969. Biomass of desert winter annual plant populations in southern Nevada. *Oikos* 20:261–273.
- . 1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. *Ecology* 55:856–863.
- BISWELL, H. H. 1956. Ecology of California grasslands. *Journal of Range Management* 9:19–24.
- BOOTH, T. A. and A. J. RICHARDS. 1976. Studies in the *Hordeum murinum* aggregate. 1. Morphology. *Journal of the Linnean Society, Botany* 72:149–159.
- BORCHERT, M. I. and S. K. JAIN. 1978. The effect of rodent seed predation on four species of California annual grasses. *Oecologia* 33:101–114.
- BOWERS, J. E. 1989. A debt to the future: scientific achievements of the Desert Laboratory, Tucson, Arizona. *Desert Plants* 10:9–12, 35–47.
- and R. M. TURNER. 1985. A revised vascular flora of Tumamoc Hill, Tucson, Arizona. *Madroño* 32:225–252.
- BOWERS, M. A. 1987. Precipitation and the relative abundances of the desert winter annuals; a 6-year study in the northern Mojave Desert. *Journal of Arid Environments* 12:141–149.
- BRITTON, N. L. and R. H. KEARNEY. 1894. An enumeration of the plants collected by Dr. Timothy E. Wilcox, U.S.A., and others in southeastern Arizona during the years 1892–1894. *Transactions of the New York Academy of Sciences* 14: 21–44.
- BROWN, C. J. and A. A. GUBB. 1986. Invasive alien organisms in the Namib Desert, Upper Karroo and the arid and semi-arid savannas of western southern Africa. Pp. 93–108 in A. W. Macdonald, F. J. Kruger, and A. A. Ferrar (eds.), *The ecology and management of biological invasions in southern Africa*. Oxford University Press, New York.
- BROWN, D. E. and R. A. MINNICH. 1986. Fire and changes in creosote bush scrub of the western Sonoran Desert, California. *American Midland Naturalist* 116: 411–422.
- BUFKIN, D. 1981. From mud village to modern metropolis: the urbanization of Tucson. *Journal of Arizona History* 22:63–98.
- CANNON, W. A. 1911. The root habits of desert plants. *Publications of the Carnegie Institute of Washington* no. 131.
- CHEAM, A. H. 1984. Allelopathy in buffel grass (*Cenchrus ciliaris* L.). Part II. Site of release and distribution of allelochemical in the soil profile. *Australian Weeds* 3:137–139.
- CHRISTIE, E. K. 1975. Physiological responses to semiarid grasses. II. The pattern of root growth in relation to external phosphorus concentration. *Australian Journal of Agricultural Research* 26:437–446.
- CONERT, H. J. and A. M. TURPE. 1974. Revision der Gattung *Schismus* (Poaceae: Arundinoideae: Danthonieae). *Abh. Senckenberg. Naturf. Ges.* no. 532.

- CORRELL, D. S. and M. C. JOHNSTON. 1970. Manual of the vascular plants of Texas. Texas Research Foundation, Renner, TX.
- COVILLE, F. V., N. L. BRITTON, J. M. MACFARLANE, and G. PINCHOT. 1903. Carnegie Institute of Washington Year Book, Vol. 1.
- COX, J. R., M. H. MARTIN-R, F. A. IBARRA-F, J. H. FOURIE, N. F. G. RETHMAN, and D. G. WILCOX. 1988. The influence of climate and soils on the distribution of four African grasses. *Journal of Range Management* 41:127-139.
- DANIN, A. 1976. Roadside vegetation in Israel. *Phytoparasitica* 4:143.
- DAVIDSON, A. 1907. The changes in our weeds. *Bulletin of the Southern California Academy of Sciences* 6:11-12.
- DAVISON, A. W. 1971. The ecology of *Hordeum murinum* L. II. The ruderal habit. *Journal of Ecology* 59:493-506.
- DEGROOTE, D. K. and R. T. SHERWOOD. 1984. In vitro sexual and apomictic embryo sac development in *Cenchrus ciliaris*. *Canadian Journal of Botany* 62:2053-2057.
- DELISLE, D. G. 1963. Taxonomy and distribution of the genus *Cenchrus*. *Iowa State College Journal of Science* 37:259-351.
- DE VITA, J. 1979. Mechanisms of interference and foraging among colonies of the harvester ant *Pogonomyrmex californicus* in the Mojave Desert. *Ecology* 60:729-737.
- DIAMOND, J. 1988. Why was post-Pleistocene development of human societies slightly more rapid in the Old World than in the New? Pp. 25-30 in R. C. Carlisle (ed.), *Americans before Columbus: ice-age origins*. *Ethnology Monographs* no. 12, Department of Anthropology, University of Pittsburgh.
- EARLE, W. H. 1973. A new plant for Arizona, *Dimorphotheca aurantiaca*. *Saguaro-land Bulletin* 27:56-57.
- ELLENBERG, H. 1988. *Vegetation ecology of central Europe*, 4th ed. (G. K. Strutt, transl.) Cambridge University Press, New York.
- FARUQI, S. A. 1981. Studies on the Libyan grasses. VII. Additional note on *Schismus arabicus* and *S. barbatus*. *Pakistan Journal of Botany* 13:225.
- and H. B. QURAIISH. 1979. Studies on Libyan grasses. V. Population variability and distribution of *Schismus arabicus* and *S. barbatus* in Libya. *Pakistan Journal of Botany* 11:167-172.
- FEINBRUN-DOTHAN, N. 1986. *Flora Palaestina*, Part 4. Israel Academy of Sciences and Humanities, Jerusalem.
- FLORY, E. L. and C. G. MARSHALL. 1942. Regrassing for soil protection in the Southwest. *USDA Farmer's Bulletin*, no. 1913.
- FRENKEL, R. E. 1977. Ruderal vegetation along some California roadsides. University of California Press, Berkeley.
- GOLDBERG, D. E. and R. M. TURNER. 1986. Vegetation change and woody plant demography in permanent plots in the Sonoran Desert. *Ecology* 67:695-712.
- GOULD, F. 1946. Arizona plant records. Leaflets in *Western Botany* 4:247-249.
- . 1949. Arizona plant records—II. Leaflets in *Western Botany* 5:167-170.
- and R. MORAN. 1981. *The grasses of Baja California, Mexico*. San Diego Society of Natural History Memoir 12.
- GRIFFITHS, D. 1904. Range investigations in Arizona. *USDA Bureau of Plant Industry Bulletin* no. 67.
- . 1910. A protected stock range in Arizona. *USDA Bureau of Plant Industry Bulletin* no. 177.
- HAMILTON, F. L. 1933. *The desert garden*. Frances L. Hamilton, Phoenix, AZ.
- HEADY, H. F. 1977. Valley grassland. Pp. 491-514 in M. G. Barbour and J. Major (eds.), *Terrestrial vegetation of California*. John Wiley and Sons, New York.
- HORTON, J. S. 1964. Notes on the introduction of deciduous tamarisk. *USDA Forest Service, Rocky Mountain Forest and Range Experiment Station Research Paper RM-16*.
- HUBL, E. and W. HOLZNER. 1982. Iran. Pp. 257-266 in W. Holzner and N. Numata (eds.), *Biology and ecology of weeds*. Dr. W. Junk, The Hague.

- HULBERT, L. C. 1955. Ecological studies of *Bromus tectorum* and other annual brome grasses. *Ecological Monographs* 25:181-213.
- HUSSAIN, F., H. H. NAQVI, and I. ILAHI. 1982. Interference exhibited by *Cenchrus ciliaris* L. and *Bothriochloa pertusa* (L.) A. Camus. *Bulletin of the Torrey Botanical Club* 109:513-523.
- INOUE, R. S. 1980. Density-dependent germination response by seeds of desert annuals. *Oecologia* 46:235-238.
- , G. S. BYERS, and J. H. BROWN. 1980. Effects of predation and competition on survivorship, fecundity and community structure of desert annuals. *Ecology* 61:1344-1351.
- JACKSON, L. E. 1985. Ecological origins of California's mediterranean grasses. *Journal of Biogeography* 12:349-361.
- JUHREN, M., F. W. WENT, and E. PHILLIPS. 1956. Ecology of desert plants. IV. Combined field and laboratory work on germination of annuals in the Joshua Tree National Monument. *Ecology* 37:318-330.
- KARPISCAK, M. M. 1980. Secondary succession of abandoned field vegetation in southern Arizona. Ph.D. dissertation. University of Arizona, Tucson.
- KERNEY, T. H. 1931. Plants new to Arizona. *Journal of the Washington Academy of Sciences* 21:63-80.
- . 1954. Further additions to the known flora of Arizona. *Leaflets in Western Botany* 7:165-175.
- KHOSHOO, T. N. 1955. Biosystematics of the *Sisymbrium irio* complex. *Nature* 176: 608.
- KNIGHT, R. S. 1986. A comparative analysis of fleshy fruit displays in alien and indigenous plants. Pp. 171-178 in I. A. W. Macdonald, F. J. Kruger, and A. A. Ferrar (eds.), *The ecology and management of biological invasions in southern Africa*. Oxford University Press, Cape Town.
- LE FLOC'H, E., H. N. LE HOUEROU, and J. MATHEZ. 1990. History and patterns of plant invasion in northern Africa. Pp. 105-133 in F. Di Castri, A. J. Hanson, and M. Debussche (eds.), *Biological invasions in Europe and the Mediterranean Basin*. Kluwer Academic, Boston.
- LE HOUEROU, H. N. In press. Plant invasion in the rangelands of the isoclimatic Mediterranean Zone. In R. H. Groves and F. Di Castri (eds.), *Biogeography of Mediterranean invasion*. Cambridge University Press, New York.
- LORIA, M. and I. NOY-MEIR. 1980. Dynamics of some annual populations in a desert loess plain. *Israel Journal of Botany* 28:211-225.
- MACK, R. N. 1981. Invasion of *Bromus tectorum* into western North America: an ecological chronicle. *Agro-Ecosystems* 7:145-165.
- . 1986. Alien plant invasion into the Intermountain West. Pp. 191-213 in H. A. Mooney and J. A. Drake (eds.), *Ecology of biological invasions of North America and Hawaii*. Springer-Verlag, New York.
- 'T MANNETJE, L., S. J. COOK, and J. H. WILDIN. 1983. The effects of fire on a buffel grass and siratro pasture. *Tropical Grasslands* 17:30-39.
- MARTIN, M. M. and J. HARDING. 1982. Estimates of fitness in *Erodium* populations with intraspecific and interspecific competition. *Evolution* 36:1290-1298.
- MARTIN, P. S. and R. KLEIN. 1984. Quaternary extinctions: a prehistoric revolution. University of Arizona Press, Tucson.
- MASON, C. T., JR. 1960. Notes on the flora of Arizona II. *Leaflets in Western Botany* 9:87-88.
- MAYEUX, H. S., JR. and W. T. HAMILTON. 1983. Response of common goldenweed (*Isocoma coronopifolia*) and buffelgrass (*Cenchrus ciliaris*) to fire and soil-applied herbicides. *Weed Science* 31:355-360.
- MCCLATCHIE, A. J. 1900. Green-manuring plants for orchards. Pp. 65-68 in University of Arizona Agriculture Experiment Station Bulletin no. 34.
- . 1901. Wild barley. Pp. 287-290 in University of Arizona Agriculture Experiment Station Bulletin no. 38.

- MCKELL, C. M., J. R. ROBISON, and J. MAJOR. 1962. Ecotypic variation in medusahead, an introduced annual grass. *Ecology* 43:686-698.
- MOTT, J. J. 1982. Fire in improved pastures of Northern Australia. *Tropical Grasslands* 16:97-100.
- NAVEH, Z. 1967. Mediterranean ecosystems and vegetation types in California and Israel. *Ecology* 48:443-459.
- PARSONS, J. J. 1970. The "Africanization" of the New World tropical grasslands. Pp. 141-153 in H. Blume and K. H. Schroder (eds.), *Beitrage zur Geographie der Tropen und Subtropen*, Geographische Studien 34. Geographischen Instituts der Universitat Tubingen, Tubingen.
- PIEMEISEL, R. L. 1932. Weedy abandoned lands and the weed hosts of the beet leafhopper. USDA Circular no. 229.
- . 1951. Causes affecting change and rate of change in a vegetation of annuals in Idaho. *Ecology* 32:53-72.
- POPAY, A. I. 1981. Germination of seeds of 5 annual species of barley grass. *Journal of Applied Ecology* 18:547-558.
- RICKARD, W. H. and R. H. SAUER. 1982. Self revegetation of disturbed ground in the deserts of Nevada and Washington, USA. *Northwest Science* 56:41-47.
- RISCH, S. J. and C. R. CARROLL. 1986. Effects of seed predation by a tropical ant on competition among weeds. *Ecology* 67:1319-1327.
- RISSING, S. W. 1986. Indirect effects of granivory by harvester ants: plant species composition and reproductive increase near ant nests. *Oecologia* 68:231-234.
- ROBBINS, W. W. 1940. Alien plants growing without cultivation in California. University of California Agriculture Experiment Station Bulletin no. 637.
- ROBERTS, H. A. 1981. Seed banks in soils. *Advances in Applied Biology* 6:1-55.
- . 1986. Seed persistence in soil and seasonal emergence in plant species from different habitats. *Journal of Applied Ecology* 23:639-656.
- ROGERS, G. F. and J. STEELE. 1980. Sonoran Desert fire ecology. Pp. 15-19 in M. A. Stokes and J. H. Dieterich (tech. coords.), *Proceedings of the fire history workshop*. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-81.
- ROSSITER, R. C. 1966. Ecology of the Mediterranean annual-type pasture. *Advances in Agronomy* 18:1-50.
- SALISBURY, E. 1964. *Weeds and aliens*. Collins, London.
- SCHMIDT, W. E. 1969. The African sumac in Arizona. *California Horticultural Journal* 30:19-21.
- SHREVE, F. 1951. *Vegetation of the Sonoran Desert*. Publications of the Carnegie Institute of Washington, no. 591.
- SOHOLT, L. F. 1973. Consumption of primary production by a population of kangaroo rats (*Dipodomys merriami*) in the Mojave Desert. *Ecological Monographs* 43:357-376.
- SPALDING, V. M. 1909. *Distribution and movements of desert plants*. Publications of the Carnegie Institute of Washington, no. 113.
- STAMP, N. E. and R. D. OHMART. 1978. Resource utilization by desert rodents in the lower Sonoran Desert. *Ecology* 59:700-707.
- SZAREK, S. R., S. D. SMITH, and R. D. RYAN. 1982. Moisture stress effects on biomass partitioning in two Sonoran Desert annuals. *American Midland Naturalist* 108:338-345.
- TADROS, T. M. and B. A. M. ATTA. 1959. The plant communities of barley fields and uncultured desert areas of Mareotis (Egypt). *Vegetatio* 8:161-175.
- TEVIS, L., JR. 1958. Germination and growth of ephemerals induced by sprinkling a sandy desert. *Ecology* 39:681-688.
- THORNBUR, J. J. 1903. *University of Arizona Agriculture Experiment Station Annual Report*.
- . 1906. *Alfilaria, Erodium cicutarium*, as a forage plant in Arizona. Pp. 27-58 in *University of Arizona Agriculture Experiment Station Bulletin* no. 52.

- . 1909. Vegetation groups of the Desert Laboratory domain. Pp. 103–112 in V. M. Spalding (ed.), *Distribution and movements of desert plants*. Publications of the Carnegie Institute of Washington, no. 113.
- . 1910. Grazing ranges of Arizona. Pp. 245–360 in *University of Arizona Agriculture Experiment Station Bulletin* no. 65.
- TISDALE, E. W., M. HIRONAKA, and M. A. FOSBERG. 1965. An area of pristine vegetation in Craters of the Moon National Monument, Idaho. *Ecology* 46:349–352.
- TITZ, W. 1969. Chromosomenzahlen dreier europaischer Cruciferen. *Berichte der Deutschen Botanischen Gesellschaft* 82:553–555.
- TOUMEY, J. J. 1897. Something about weeds. *University of Arizona Agriculture Experiment Station Bulletin* no. 22.
- TSVELEV, N. N. 1983. Grasses of the Soviet Union. B. R. Sharma (trans.). Amerind Publishing, New Dehli.
- TURNAGE, W. V. and A. C. HINCKLEY. 1938. Freezing weather in relation to plant distribution in the Sonoran Desert. *Ecological Monograph* 8:530–550.
- TURNER, R. M. and J. E. BOWERS. 1988. Long-term changes in populations of *Carnegiea gigantea*, exotic plant species and *Cercidium floridum* at the Desert Laboratory, Tumamoc Hill, Tucson, Arizona. Pp. 445–455 in *Arid lands: today and tomorrow*, Proceedings of the international arid lands research and development conference, October 1985, Tucson, Arizona. Westview Press, Boulder, CO.
- VVEDENSKII, A. I. 1974. Genus 831 *Erodium* L'Her. Pp. 49–56 in B. K. Shishkin and E. G. Bobrov (eds.), *Flora of the U.S.S.R.*, Vol. XIV, Geraniales, Sapindales, Rhamnales (transl. R. Lavoott). Keter Publ. House Jerusalem Ltd., Jerusalem.
- WAGONER, J. J. 1952. History of the cattle industry in southern Arizona, 1540–1940. *University of Arizona Social Sciences Bulletin* no. 20.
- WEBB, D. A. and A. O. CHATER. 1968. *Erodium* L'Her. Pp. 199–204 in T. G. Tutin, V. H. Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters, and D. A. Webb (eds.), *Flora Europaea*, Vol. 2, Rosaceae to Umbelliferae. Cambridge University Press, Cambridge.
- WENT, F. W. 1948. Ecology of desert plants. I. Observations on germination in the Joshua Tree National Monument, California. *Ecology* 29:242–253.
- . 1949. Ecology of desert plants. II. The effect of rain and temperature on germination and growth. *Ecology* 30:1–13.
- and M. WESTERGAARD. 1949. Ecology of desert plants. III. Development of plants in the Death Valley National Monument, California. *Ecology* 30:26–38.
- WESTER, L. 1981. Composition of native grasslands in the San Joaquin Valley, California. *Madroño* 28:231–241.
- WILSON, B. J. and A. A. DUFF. 1984. Dynamics of weed seedling emergence in wheat growing soils. Pp. 162–163 in R. W. Madin (ed.), *Proceedings of the seventh Australian weeds conference*, Vol. 1.
- WU, K. K. and S. K. JAIN. 1978. Genetic and plastic responses in geographic differentiation of *Bromus rubens* populations. *Canadian Journal of Botany* 56: 873–879.
- and ———. 1979. Population regulation in *Bromus rubens* and *B. mollis*: life cycle components and competition. *Oecologia* 39:337–358.
- YENSEN, D. L. 1981. The 1900 invasion of alien plants into southern Idaho. *Great Basin Naturalist* 41:176–183.
- YOUNG, J. A., R. A. EVANS, and J. MAJOR. 1972. Alien plants in the Great Basin. *Journal of Range Management* 25:294–201.
- ZOHARY, M. 1950. The segetal plant communities of Palestine. *Vegetatio* 2:387–411.
- . 1972. *Flora Palaestina*, Part 2. Platanaceae to Umbelliferae. Israel Academy of Sciences and Humanities, Jerusalem.

———. 1973. Geobotanical foundations of the Middle East. Gustav Fischer Verlag, Stuttgart.

(Received 4 Sept 1990; revision accepted 23 Dec 1990.)

APPENDIX I.

STATUS AND HISTORY OF SELECTED EXOTICS AT THE DESERT LABORATORY, TUCSON, ARIZONA

The vouchers cited below are deposited at ARIZ. It is difficult to determine when most of these introductions occurred. An exotic species may have been established on our study area many years before its initial documentation.

Avena fatua L. Scattered and rare; disturbed sites along roads and in washes. Established in California by 1824 (Frenkel 1977); present in Arizona by 1902 (Thornber s.n.); first Desert Laboratory collection made in 1983 (Bowers and Turner 2222).

Brassica tournefortii Gouan. Scattered and rare; fence lines and washes. Introduced into Arizona ca. 1960 (Mason 1960); first Desert Laboratory collection made in 1978 (Turner 78-1).

Bromus rubens L. Widespread and common. Established in California by 1848 (Frenkel 1977), though not naturalizing to any appreciable extent for another 45 years (Davidson 1907); present in Tucson by 1909 (Thornber 1909) and beginning to spread to nearby "mesas" by 1910 (Thornber 1910); first Desert Laboratory collection made in 1968 (Mason and Turner 68-130). Perhaps introduced into Tucson area when sown as potential annual forage plant on Santa Rita Experimental Range in winter of 1906-1907 and 1907-1908 (Thornber 1910).

Bromus catharticus Vahl. Scattered and occasional; disturbed sites, often in low-lying areas. Present in Arizona by 1894 (Britton and Kearney 1894); first Desert Laboratory collection made in 1968 (Mason and Turner 68-131).

Caesalpinia gilliesii (Hook.) Wall. Local and rare. Wash borders near the west boundary and riparian thickets where floodwaters pond. First Desert Laboratory collection made in 1989 (Burgess 7611).

Centaurea melitensis L. Confined to landfill, where occasional. Established in California by 1824 (Frenkel 1977); present in Arizona by 1897 (Toumey 1897); first noted at Desert Laboratory in 1983.

Chenopodium murale L. Scattered and occasional; disturbed sites, often along fence lines. Established in California by 1824 (Frenkel 1977); present in Arizona by 1901 (Thornber 4433); not known from Desert Laboratory until 1983 (Bowers 2587).

Cynodon dactylon L. Scattered and locally abundant; disturbed, low-lying areas. Established in California by 1860 (Frenkel 1977); growing without cultivation in Arizona by 1891 (Toumey s.n.); known from Desert Laboratory Hill since 1909 (Spalding 1909).

Dimorphotheca sinuata DC. Scattered and rare; usually along washes. Cultivated in Arizona since the 1940's, naturalized in various locations by the 1970's (Earle 1973); first Desert Laboratory collection made in 1978 (Turner and Goldberg 78-8).

Eragrostis lehmanniana Nees. Local and common; usually on disturbed sites but occasionally elsewhere. Introduced at Tucson in 1934 by the Soil Conservation Service (Flory and Marshall 1942); well established along roadsides in Tucson by 1946 (Gould 1946); first Desert Laboratory collection made in 1983 (Bowers 2703).

Erodium cicutarium (L.) L'Her. Widespread and common. Established in California by 1824 (Frenkel 1977); present in Arizona by 1866, no doubt introduced into the state by sheep from California (Thornber 1906) and also sown deliberately

by at least one rancher (Arizona Daily Star, June 13, 1880); known from the San Pedro Valley since 1880 (Arizona Daily Star, February 10, 1880), the Tucson area since 1903 (Thornber 1903) and from Desert Laboratory since 1906 (Spalding 1909).

- Hordeum murinum* L. subsp. *glaucum* (Steud.) Tzvelev. Widespread and occasional. Established in California by 1824 (Frenkel 1977); present in Arizona by 1894 (Britton and Kearney 1894); established in the Salt River valley by 1897 (Toumey 1897) and a noxious weed there by 1901 (McClatchie 1901); known from Desert Laboratory since 1906 (Spalding 1909); uncommon in the Tucson area until at least 1910 (Thornber 1910). Three major taxa have been defined in the *Hordeum murinum* group. On the basis of anther length, both *H. murinum* subsp. *leporinum* and *H. murinum* subsp. *glaucum* have been collected on the Desert Laboratory grounds. Lodicules are considered a more reliable diagnostic character (Baum and Bailey 1984a, b), and in this feature our collections conform to *H. murinum* subsp. *glaucum*.
- Lactuca serriola* L. Scattered and rare; disturbed sites, most often in washes. Established in California by 1860 (Frenkel 1977); present in Arizona by 1905 (Thornber 5572); first noted on Desert Laboratory grounds in 1983.
- Lantana horrida* H.B.K. Scattered and rare. An ornamental commonly cultivated in and around Tucson; first Desert Laboratory collection made in 1983 (Bowers 2704).
- Lepidium oblongum* Small. Local, occasional to common. Introduced into Arizona by 1902 (Thornber s.n.); first Desert Laboratory collection made in 1983 (Bowers and Turner 2225).
- Malva parviflora* L. Scattered and rare; low-lying disturbed sites. Established in California by 1824 (Frenkel 1977); present in Tucson by 1891 (Toumey s.n.); first Desert Laboratory collection made in 1978 (Turner 78-5).
- Matthiola longipetala* (Vent.) DC. ssp. *bicornis* Sibth. & Sm. Scattered and rare; on landfill and fence lines. Introduced into Tucson ca. 1905 and escaping from cultivation (Thornber 1909); first Desert Laboratory collection made in 1983 (Turner and Goldberg 78-13).
- Melia azederach* L. Local and rare on landfill. Common ornamental in and around Tucson; first Desert Laboratory collection made in 1983 (Turner 83-4).
- Melilotus indicus* (L.) All. Local and rare; moist sites near ponds. Established in California by 1848 (Frenkel 1977); present in Arizona by 1891 (Toumey s.n.); common weed in southern Arizona by 1900 (McClatchie 1900); first Desert Laboratory collection made in 1983 (Bowers and Turner 2210).
- Molucella laevis* L. Scattered and rare; usually in moist sites. An ornamental commonly cultivated in and around Tucson; first Desert Laboratory collection made in 1979 (Turner and VanHylckama 79-64).
- Nicotiana glauca* Grah. Scattered and rare; usually in moist sites, but also on steep slopes with southerly aspects. Established in California by 1848 (Frenkel 1977); cultivated in Tucson by 1891 and escaping from cultivation by 1904 (Thornber 480); first Desert Laboratory collection made in 1983 (Turner 83-11).
- Opuntia microdasys* (Lehm.) Pfeiffer. Local and rare; gravelly flats near the west boundary; first noted on Desert Laboratory grounds in 1984.
- Parkinsonia aculeata* L. Scattered and rare; most common on sanitary landfill. Cultivated in and around Tucson; first Desert Laboratory collection made in 1968 (Warren and Turner 68-155).
- Pennisetum ciliare* (L.) Link. Scattered, rare to abundant. Introduced to Arizona by Soil Conservation Service ca. 1938, spreading from plantings by 1954 (Kearney 1954); first Desert Laboratory collection made in 1968 (Warren and Turner 68-11).
- Pennisetum setaceum* (Forsk.) Chiov. Local and occasional. Usually in disturbed sites where runoff collects, also in crevices of some basalt outcrops; first Desert Laboratory collection made in 1983 (Bowers 2754).

- Phacelia campanularia* Gray. Local and rare; not established. A California native, doubtless spreading to our area from nearby plantings; first Desert Laboratory collection made in 1983 (*Bowers and Turner 2226*).
- Phalaris minor* Retz. Local and occasional; moist sites. Introduced into California by 1882 (Robbins 1940); present in Arizona by 1913 (*Thorner s.n.*); first Desert Laboratory collection made in 1978 (*Turner and Goldberg 78-18*).
- Polygomon monspeliensis* (L.) Desf. Local and occasional; moist sites. Established in California by 1848 (Frenkel 1977); present in Arizona by 1891 (*Toumey s.n.*); first Desert Laboratory collection made in 1978 (*Turner and Goldberg 78-20*).
- Rhus lancea* L. Local and rare; moist areas along washes. Introduced into California in 1919; first planted in Tucson in 1928 (Schmidt 1969); first Desert Laboratory collection made in 1984 (*Bowers 2970*).
- Salsola australis* R. Brown. Scattered and common; abundant on landfill. Introduced into U.S. in 1886 in flax seed sown in South Dakota and established in California by 1895 (Robbins 1940); first collected in Tucson in 1892 (*Toumey s.n.*). Oddly, in 1897 Toumey wrote, "There is no direct evidence that this weed had yet found its way into Arizona," and in 1904, Griffiths described *Salsola* as common along railway lines in northern Arizona but added, "so far as known it does not occur in the southern part of Arizona at all." In any case by 1913, *Salsola* was apparently well established in Tucson (*Thorner 7305, Thorner s.n.*). The first Desert Laboratory collection was made in 1968 (*Warren and Turner 68-160*).
- Schismus arabicus* Nees. Widespread, common to abundant. Present in Arizona by 1933 (*Peebles 9098*); first Desert Laboratory collection made in 1968 (*Mason and Turner 68-128*).
- Schismus barbatus* (L.) Thell. Widespread, common to abundant. First collected in Arizona in 1926, naturalized in central part of state by 1931 (Kearney 1931) and in southern part by 1949 (Gould 1949); first Desert laboratory collection made in 1983 (*Bowers 2455*). Apparently not introduced into California until 1935 (Robbins 1940). It is unclear whether *S. arabicus* and *S. barbatus* both occur in our study area. Faruqi and Quaraish (1979) and Faruqi (1981) found that in Libya, intermediate forms apparently derived from hybridization and backcrossing between the two taxa have been stabilized by high rates of autogamy. They concluded that there is no justification for regarding *S. barbatus* and *S. arabicus* as separate species. Specimens from the Desert Laboratory fit *S. barbatus* as defined by Conert and Turpe (1974). A review of the North American material seems in order.
- Sisymbrium irio* L. Widespread and occasional. Present in Arizona by 1909 (*Thorner s.n.*), in California by 1918 (Robbins 1940); abundant in the Phoenix area by 1933 (Hamilton 1933); first Desert Laboratory collection made in 1968 (*Warren and Turner 68-47*).
- Sisymbrium orientale* L. Scattered and occasional; along washes. Present in Arizona by 1931 (*Harrison et al. 7554*); first Desert Laboratory collection made in 1978 (*Turner and Goldberg 78-11*).
- Sonchus oleraceus* L. Scattered and rare; often along washes. Established in California by 1824 (Frenkel 1977); present in Tucson by 1897 (Toumey 1897); first Desert Laboratory collection made in 1983 (*Bowers 2502*).
- Tamarix ramosissima* Ledeb. Occasional at ponds in clay quarries. First collected in Arizona in 1901 (Horton 1964); first Desert Laboratory collection made in 1968 (*Warren and Turner 68-120*). A cultivated species that has become widely naturalized in the Southwest.